THE REPRODUCTION AND EARLY LIFE HISTORY OF THE GASTROPOD *CYMATILESTA SPENGLERI* (PERRY) (FAM. CYMATIDAE).

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(*Communicated by Miss I. Bennett.*)

(Plate ix; 17 Text-figures.)

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Synopsis.

C. spengleri shows clear sexual dimorphism. Pairing occurs in the spring, and the female produces a characteristic egg mass. Early development through a yolky veliger to metamorphosis takes place within the egg mass, with escape of the young to a free-living benthic existence at 16 days. The pattern of reproduction and early life history is typical for a mesogastropod prosobranch.

Introduction.

Many workers have made contributions to our knowledge of the life histories of prosobranch gastropods, and the details that have emerged have been clearly summarized by Lebour (1937) and Thorson (1946, 1950). The majority of investigations, however, have been of European and American species and the life histories of the tropical and subtropical marine prosobranchs, especially those of the eastern Pacific, remain largely unrecorded. Many of the families occurring in this region are represented in the molluscan fauna of the eastern Australian seaboard, among them the Cymatidae (triton shells). The following account of the early life history of *Cymatilesta spengleri* is the first for a member of this family.

Sex Difference and Spawning Habits.

C. spengleri is typical of the smaller cymatids, an average adult specimen measuring 4–5 inches in length. Like all prosobranchs, the species is dioecious, and a degree of sexual dimorphism is evident in addition to the presence of the penis in the male. The female is slightly the larger, with a thicker and less sharply conical spire and a much thicker rim to the mouth of the shell. Adults of both sexes are found in considerable numbers near the low water mark on rocky shores in the vicinity of Sydney. Breeding takes place in the spring (October–November), the animals being found associated in pairs at this time, and egg masses are attached to shaded rock faces just above the extreme low level of spring tides. The extent of the sublittoral range of the species and the possibility of sublittoral breeding are undecided, but an indication of a more than littoral distribution is given by the preponderance of fully grown adults on the shore. As will be seen below, the species has no planktonic larval stage and hatches as an almost complete miniature adult. Stages of growth leading to the adult must take place mainly in sublittoral waters, and it may even be that the later migration of adults to the shore is a breeding migration.

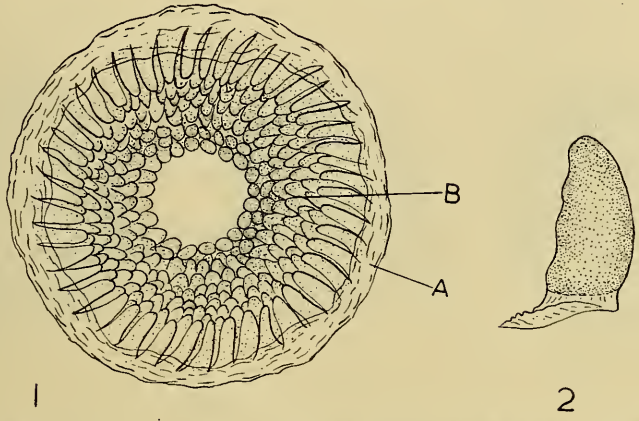
Copulation has not been observed in *C. spengleri*, but must considerably precede spawning by the female, since egg laying occurs in isolation. On November 11, 1958, Miss I. Bennett, of the Zoology Department, University of Sydney, and myself, while collecting at Long Reef, Collaroy, north of Sydney, found in addition to several egg masses suspected to be of this species, a female in process of spawning an identical egg mass. Both egg mass and parent are shown in Plate ix.

The Egg Mass.

When complete, the egg mass (Pl. ix, A, B; Text-fig. 1) is circular in outline, cup-shaped, and glued to the rock by its flat base. It consists of a spiral of conical egg capsules, beginning in the centre of the mass with the capsules vertically placed and

continuing outwards and upwards until the capsules at the rim of the cup are horizontally placed. The outer surface of the mass is made up of a series of thin, horny, overlapping, transparent plates, with the close-packed capsules firmly attached to their inner surfaces.

The female fashions the egg mass within the mouth of the shell, and the diameter of the two correspond. The region of greatest height of the mass is formed at the anterior rim of the shell, the opposite lowest region lying under the first coil of the visceral spire. The mode of construction of the mass is not yet clear, but the individual egg capsules are extruded from the mantle cavity already fully formed. The horny plates must therefore be produced and glued together and the capsules attached to



Text-fig. 1, 2. *Cymatilesta spengleri*: 1. Egg mass, natural size. 2. Egg capsule, × 2. A, horny plates of surface layer; B, egg capsule.

them by a means accessory to the genital system. Each of the several hundred egg capsules is a horny, transparent, flattened, blunt ended cone curving outwards at the base (Text-fig. 2). Within it is a clear jelly in which lie several hundred eggs, each creamy white in colour, but imparting to the whole egg mass a delicate pale orange tint.

Methods.

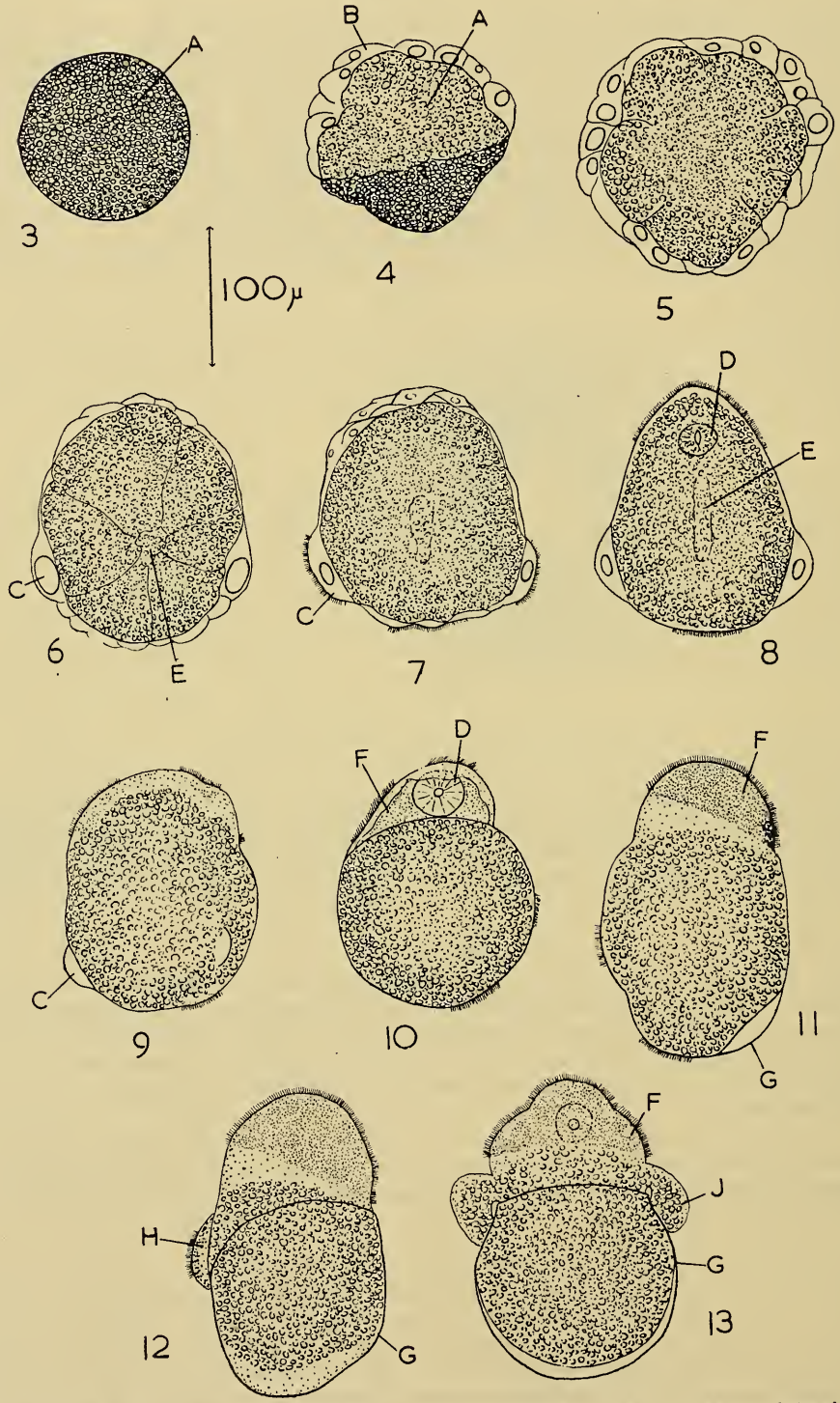
The newly spawned egg mass was maintained in a bowl of clean sea water in the laboratory. With constant aeration and a change of sea water every three days, the embryos within the egg capsules developed steadily, feeding on yolk reserves, for 16 days, when hatching took place. It did not prove possible to culture the hatched embryo further, but by this time they had almost completed metamorphosis and were benthic in habit.

At intervals during the 16-day period, capsules were removed from the mass and slit open to release embryos for observation alive. Camera lucida drawings were made of specimens narcotized with 10% alcohol, magnesium chloride proving ineffective at normal narcotic concentration.

External Features of Development.

The fertilized egg of *C. spengleri* is opaque, spherical, 120μ in diameter, creamy white in colour, and covered by a very thin egg membrane closely adherent to the egg (Text-fig. 3). Before cleavage begins the membrane disappears, and the cleavage blastomeres are only loosely held together in the early cleavage stages. The egg is very yolky, large yolk globules being uniformly distributed throughout the cytoplasm.

The first two cleavages are almost equal, but the third is very unequal, giving a quartette of small micromeres at the animal pole and four large yolky macromeres at the vegetal pole. Cleavage follows the normal spiral pattern, but all the micromeres



Text-fig. 3-13. *Cymatilesta spengleri*: 3. Fertilized egg. 4. 5 hr. blastula, lateral view. 5. 14 hr. gastrula, lateral view. 6. Early trochophore, 17 hr., dorsal view. 7. Trochophore, 20 hr., dorsal view. 8. Trochophore, 24 hr., ventral view. 9. Early veliger, 36 hr., dorsal view. 10. Veliger, 2½ days, dorsal view. 11. Veliger, 3½ days, ventral view. 12. Veliger, 6 days, dorsal view. 13. Veliger, 8 days, dorsal view.

A, yolk; B, micromeres; C, lateral ciliated cells; D, stomodaeum; E, archenteron; F, oral hood; G, shell; H, foot; J, yolk masses.

are small, the major part of the yolk residing in the four vegetal pole macromeres. A solid blastula with a cap of animal pole micromeres is found about five hours after first cleavage.

Gastrulation proceeds wholly by epiboly, the micromeres multiplying and spreading over the macromeres (Text-fig. 4), at first equally on all sides, but later more rapidly dorsally and posteriorly, so that eventual closure of the blastopore takes place mid-ventrally from behind forwards, the anterior end of the blastopore remaining open as the future mouth. By the time gastrulation is complete the large yolky (endoderm) cells have begun to increase in number and the embryo shows some increase in size, though still retaining a spherical shape (Text-fig. 5). At this stage it is about 14 hours old.

During the next three hours the embryo elongates along the antero-posterior axis and becomes ovoid, pointed anteriorly and blunt posteriorly (Text-fig. 6). The superficial layer of yolk-free cells remains very thin, while the endoderm cells are further increased in number and can now be seen to surround a central space, the archenteron. On either side at the widest part of the embryo one of the superficial cells becomes enlarged and projects above the general surface, showing a large clear nucleus. By the time the embryo is 20 hours old these cells have become ciliated, and a further area of short cilia has appeared at the posterior end (Text-fig. 7). At the anterior end multiplication of the superficial cells is beginning, giving a layer more than one cell thick. The embryo now corresponds to a trochophore in which, associated with the presence of yolk, the larval organs are largely suppressed.

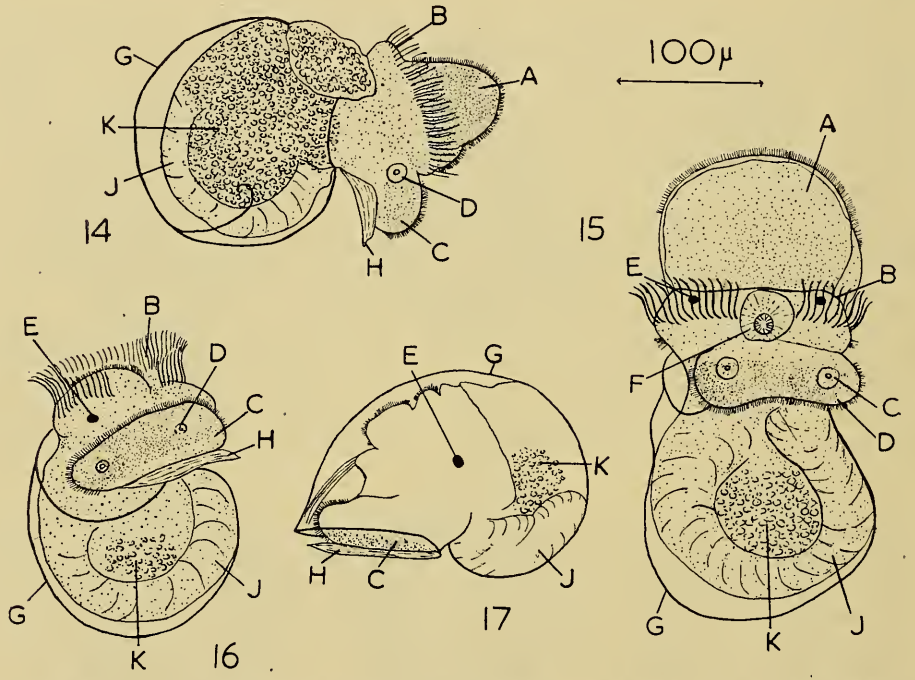
With further development the outline of the trochophore becomes better defined, the anterior end becoming more pointed. The cilia on the large lateral cells disappear, but by 24 hours a new ciliated area is present at the anterior end (Text-fig. 8). The outline of a cylindrical stomodaeum can also be seen, while the archenteron now shows as a central cylindrical space running along the antero-posterior axis, at right angles to the stomodaeum.

In the succeeding 36 hours (Text-fig. 9, 10) very little increase in size takes place, but the shape of the embryo changes in various ways. The main mass of the body containing the yolky endoderm becomes spherical and sharply demarcated from the anterior ciliated region, which broadens as a flattened oral hood overlying the stomodaeum and bearing short cilia on its convex upper (dorsal) surface. The cilia beat vigorously, driving a current backwards over the body, but cause no movement through the jelly at this stage. Neither is there any muscular movement. The posterior patch of cilia is displaced towards the left as a result of asymmetrical growth of the body, and a further patch develops laterally on the same side. The significance of these cilia is obscure.

The embryo now begins to increase in length, in size of the oral hood and in clarity of definition of the stomodaeum, which now has a ciliated lumen (Text-fig. 11). The remainder of the body remains opaque and yolky, obscuring the internal changes taking place. The 3½-day embryo, however, shows one new surface feature in the presence of a small cap shell at the posterior end of the body, towards the right side, secreted by an ectodermal thickening, the shell gland.

During the next three days, with little further increase in the size of the embryo, the shell spreads anteriorly over the dorsal surface and also downwards over the posterior end of the embryo as a broad cap (Text-fig. 12). The posterior and lateral cilia disappear, while a posterior fold of the body surface immediately underlying the shell marks the first origin of the mantle cavity. Mid-ventrally a transverse ciliated protuberance grows out, the rudiment of the future foot. The embryo is now clearly divided into head anterior to the shell, foot ventrally, and visceral hump covered by the shell. The yolk still obscures details of internal structure, but it is at this stage that the first muscular movement begins, a twisting of the posterior end of the visceral hump forwards and outwards towards the right, preliminary to torsion.

By the time the embryo is eight days old torsion of the visceral hump is complete (Text-fig. 13). The region joining the visceral hump to the head and foot narrows and behind it the hump becomes globular and shows the differentiating gut coiling posteriorly, then dorsally, over it. The shell also attains a globular form, with a wide mouth from which the head and foot project. Withdrawal into the shell is not possible at this stage. The oral hood is by this time deeply convex and differentiated into a narrower anterior and broader posterior part, heralding the formation of the velum. The foot increases in size as a transverse antero-posteriorly flattened projection covered on the anterior face and edges by numerous short cilia. The posterior face of the foot bears a small thin operculum. Embedded in the base of the foot on either side



Text-fig. 14-17. *Cymatilesta spengleri*: 14. Veliger, 9 days, lateral view. 15. Veliger, 10 days, ventral view. 16. Metamorphosing veliger, 16 days, ventral view. 17. Metamorphosing veliger, 16 days, lateral view, showing withdrawal into shell.

A, oral hood; B, velum; C, foot; D, otocyst; E, eye; F, stomodaeum; G, shell; H, operculum; J, intestine; K, yolk.

is a spherical, hollow otocyst containing a small, round, refractile otolith. The foot and head are now almost devoid of yolk, and the embryo appears at this stage to extrude yolk masses enclosed in a thin layer of cytoplasm from either side just anterior to the shell margin. The reason for this is not clear.

Growth and differentiation proceed rapidly over the next two days (Text-fig. 14, 15). The yolk gradually disappears in the visceral hump, with accompanying differentiation of the viscera, especially of the coiled gut, which now shows peristalsis. The shell, showing clear evidence of spiral form, enlarges and widens at the mouth, and a columella muscle faintly visible on the left side of the visceral hump in the living embryo is able to effect partial withdrawal of both head and foot into it. The foot becomes broader and its operculum larger and thicker. In the head, the anterior part of the oral hood becomes greatly enlarged and covered with short cilia dorsally, while the posterior part broadens and grows ventrally towards the stomodaeum, forming a circular rim on which are borne the long, strongly beating cilia of the velum. The velar cilia beat backwards, with typical propulsive and recovery strokes, and also in a

clockwise direction viewed from the anterior end, in such a way that metachronal waves of beating pass successively round the velar rim. The total effect of the cilia on the head is to drive the embryo forward through the jelly, and observation of an egg mass at this time gives the impression of vigorous activity.

Within the velar rim and around the stomodaeum, rudiments of the adult head are now beginning to become organized, and a pair of black eyespots is especially conspicuous on either side of this part of the head. No obvious response to unidirectional light is detectable, however, in embryos of this age.

The velum enlarges further on the twelfth day and projects as two lateral lobes from the sides of the head. Following this, a period of four days supervenes during which there are no gross changes in external form, though a gradual diminution in the remaining yolk in the visceral mass and an increase in muscular movement of all parts of the embryo indicate continuing histogenesis. The sixteenth day of development, however, yields the onset of a new period in the life history with retrogression of the "larval" organs of the embryo and hatching from the capsule. The anterior part of the oral hood is rapidly resorbed, together with the large lateral lobes of the velum, so that the head becomes bilobed and compact, with the two eyespots anteriorly and a tight velar ring around its margin (Text-fig. 16). With this change, the entire anterior end can now be withdrawn into the shell and the mouth of the shell closed by the operculum (Text-fig. 17). Locomotion is still brought about by the velar cilia, but these now beat not continuously but in coordinated short bursts, stopping and starting together. At about this time the capsule wall breaks down at the free end, apparently as a result of putrefaction, and the embryos escape rapidly from the jelly into the surrounding sea water. They are benthic in habit from the start, the ratio between the power of the reduced velum and the size of the body being too low to allow swimming except very close to the substratum. Crawling and active feeding presumably soon follow.

Discussion.

The summary of information on the life histories of British prosobranchs given by Lebour (1937) provides a background against which the life history of *C. spengleri* can be viewed. It is characteristic of the mesogastropod prosobranchs that their eggs are laid in thick-walled protective capsules filled with a gelatinous, usually nutritive medium in which the eggs float. Each egg has a very thin egg membrane which disappears early in development, and follows a course of development through spiral cleavage to a well-developed veliger larva. In these respects *C. spengleri* is typical of its group. Lebour clearly shows, however, and Thorson (1946) amply confirms, that hatching from the capsule may vary even within closely related species from the veliger stage, followed by a long planktotrophic life, to the fully metamorphosed stage. followed by a crawling benthic existence. *C. spengleri*, typical of species with a heavily yolked egg, approximates to the latter condition; but it cannot be assumed that other cymatids will have life histories lacking a planktonic stage.

Acknowledgements.

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EXPLANATION OF PLATE IX.

A, B. *Cymatilesta spengleri.* Female and egg mass (×½). C. *Cymatilesta spengleri* Veligers, 11 days.